Noorduijn, 1905. *Die Farben und Gestalts-Kanarien.* Magdeburg.
Pearl, R. and Boring, A. M., 1914. Some physiological observations regarding pluma ge patterns. *Science* N.S. XXXIX., 995.
Krizenecky, J., 1930. Ueber traumatischen Albinismus beim Geflugel. *Archiv. f. Geflugelkunde*, Jahrg 4, 5, 169–177.
Nero, R. W. 1960. Additional Notes on the Plumage of the Red-winged Blackbird. *Auk*, 77, 289–305.
Fox, H. Munro and Vevers, G., 1960. *The Nature of Animal Colours.*
Sage, B., 1955. Some further notes on plumage variations in the Mallard, *Anas platyrhynchos platyrhynchos* Linnaeus. *Bull. B.O.C.*, 75, 54–57.
Fitzherbert-Brockholes, W., 1885. Hairy variety of the Moorhen. *Zoologist* (3) 2, 321–332.
Stevenson, H., 1885. Ornithological Notes from Norfolk. *Zoologist* (3) 2, 31-32.
Forrest, H. E., 1901. Hairy-plumaged Moorhens. *Zoologist* (4) 5, 108.
Harrison, James M., 1951. Some Phylogenetic Trends in *Garrulus glandarius* (Linnaeus) and *Dendrocopos major* (Linnaeus). *Proc. Xth. Intern. Orn. Congr.* Uppsala, 168–172.
Reinig, W. F., 1927. Melanismus, Albinismus und Rufinismus. Leipzig.

Some recommendations for a revised check-list of the genera and species of grebes (Podicipitidae)

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Received 1st November, 1961

The grebes form a small, well-defined group very suitable for taxonomic study along modern lines. Rather surprisingly, the only recent check-list (not quite complete) is that of Peters (1931), though Hellmayr and Conover (1948) dealt with the numerous American forms. The present note gives some recommendations for a revised list of the genera and species of the Podicipitidae, based on a recently completed survey of the biology and morphology of the family to be published in full elsewhere, together with a detailed discussion of conclusions only mentioned or summarized briefly here. I would be most grateful for any comments on, or criticisms of this preliminary statement from interested workers, either with reference to the key problem of the biological aspects of the proposed classification or to its purely nomenclatural side.

The basic work on skins was done in the National Collection at the Bird Room of the British Museum (Natural History) by kind permission of the Director. I am indebted to the staff of the Bird Room for facilities.

PETERS' (1931) ARRANGEMENT

Peters (1931) listed thirty-nine forms which he arranged in five genera and eighteen full species. His arrangement may be summarized as follows:

Genus POLIOCEPHALUS. Subgenus TACHYBAPTUS.
Species: (1) *P. ruficollis* (ten races); (2) *P. pelzelnii* (monotypic) (3) *P. dominicus* (three races).

Subgenus POLIOCEPHALUS.
Species: (1) *P. rufopectus* (monotypic); (2) *P. poliocephalus* (two races).

Genus COLYMBUS.
Species: (1) *C. rolland* (monotypic); (2) *C. chilensis* (monotypic); (3) *C. occipitalis* (two races); (4) *C. taczanowskii* (monotypic); (5) *C. auritus* (monotypic); (6) *C. nigricollis* (three races); (7) *C. cristatus* (four races); (8) *C. grisegena* (two races).

Genus AECHMOPHORUS
Species: (1) *A. occidentalis* (monotypic); (2) *A. major* (monotypic).

Genus CENTROPELMA
Species: (1) *C. micropterum* (monotypic).

Genus PODILYMBUS
Species: (1) *P. podiceps* (three races); (2) *P. gigas* (monotypic).

SOME SUBSEQUENT TRENDS

Hellmayr and Conover (1948) arranged the New World grebes very much as Peters had done, except that (1) *Poliocephalus dominicus* (of Peters) was placed in the genus *Colymbus*, and (2) the monotypic species *Colymbus rolland* and *C. chilensis* (of Peters) were merged as *C. rolland* (two races). Other changes below the generic level, subsequent to Peters' list, included: (1) the description by Delacour (1933) of a new monotypic species of dabchick from Madagascar (*Podiceps rufolavatus*); (2) the separation of *P. novaehollandiae* from *P. ruficollis*, as the two had been found to occur together on some Australasian islands (see Mayr 1943); (3) the separation of New and Old World forms of *C. auritus* (Parkes 1952); (4) the description of a new and very distinctive race of *C. nigricollis* (under the name *C. caspicus andinus*) from the eastern Andes of northern Colombia (de Schauensee 1959). Had these facts been known to Peters, his probable course of action may have been: (1) to insert *P. novaehollandiae* (polytypic) and *P. rufolavatus* as full species between *P. ruficollis* and *P. pelzelnii;* (2) to treat *C. auritus* trinomially, and (3) to insert *C. andinus* as a full, monotypic species near *C. nigricollis*.

At the generic level, subsequent to Peters' list, there have been differences of opinion as to the status of *Poliocephalus* (of Peters), most modern authors tending to merge this in *Colymbus* (of Peters), either totally, with no subgeneric divisions, or as the subgenus *Poliocephalus* including, of course, *P. poliocephalus* (the type species) and its ally *P. rufopectus*. The subgenus *Tachybaptus* (of Peters) has tended to disappear entirely. The New World genera *Centropelma*, *Aechmophorus* and *Podilymbus* have been almost unanimously upheld, though *A. major* has been removed into *Colymbus* by Wetmore and Parkes (1954), a course approved by Storer (1960).

Another important, if purely clerical advance has been the ruling of the International Commission on Zoological Nomenclature (1956) on the *Colymbus* versus *Podiceps* controversy. As a result, the generic name *Colymbus* Linnaeus, 1758, has been declared indeterminate and suppressed in favour of *Podiceps* Latham, 1787. The latter name will be used throughout the rest of this note.

SOME COMMENTS ON A PROPOSED NEW ARRANGEMENT

My own survey of the grebes has been based primarily on external characters, chiefly head-ornamentation, but my knowledge of *Podiceps cristatus* in the wild (Simmons 1954–59 and unpublished) and of the literature of grebe behaviour and biology in general (such as is available) has been used as a check.

As I see it, the main trends in the evolution of grebes include the following:

(1) An increase in the effectiveness of head-ornamentation and pattern for visual display (including nocturnal display), by elaboration (growths such as crests, tippets, auricular fans, tufts and patches) and/or an increase in contrast between components (bill and gape marks, facial discs, etc.);

(2) A tendency towards larger size;

(3) Specialization towards a diet largely of fish;

(4) A tendency towards colonial nesting.

Bearing in mind these probable trends, and also taking into consideration taxonomic convenience and allowing for uncertainty and decided gaps in knowledge, I propose to classify the grebes in three genera, eighteen full species (both monotypic and polytypic) and three semispecies. As the latter must be treated binomially, this is in effect, from the point of view of nomenclature, equivalent to recognising twenty-one species. I have not used subgeneric names but thought it safer at present, in the case of the genus *Podiceps*, to arrange the birds in informal species groups and sub-groups (see, for example, Goodwin 1959). Later research may permit the elevation of such groups to formal subgeneric or even generic status. It might eventually prove possible to recognize six genera, each genus representing a different trend in some or all of the various directions taken in grebe evolution.

Podilymbus and Aechmophorus

The modern trend in taxonomy has been away from small genera, especially monotypic ones. In a small group such as the grebes, however, small genera would seem to be justified. Thus, though monotypic or virtually so, both the genus *Podilymbus* and the genus *Aechmophorus* are distinctive in both structure and behaviour and separable from the other grebes and each other. There is evidence that the pied-billed grebes (*Podilymbus*) are the most "primitive" (i.e. nearer in many characters to ancestral grebes) and the Western Grebe (*Aechmophorus*) the most "advanced". The two genera are best kept, therefore, at the beginning and end of the classification respectively. I agree with the authors mentioned earlier that the Great Grebe, *Podiceps major*, does not belong in the genus *Aechmophorus* (see further under *Podiceps* below).

Centropelma

The monotypic genus *Centropelma* was raised by Sclater and Salvin (1869) for the peculiar grebe *Podiceps micropterus* Gould, 1868, confined to the Titicaca basin of South America. In my opinion, this genus cannot be maintained because: (1) its supposed diagnostic characters are found in other grebes, and (2) its closest relative is clearly *Podiceps chilensis*, widespread in South America from Tierra del Fuego to southern Brazil and eastern Peru. I have, therefore, returned the Short-winged Grebe to the genus *Podiceps* in which Gould originally placed it (see further under *Podiceps* below).

Tachybaptus and Poliocephalus

A revision of the small grebes allocated by Peters (1931) to the genus *Poliocephalus* is overdue. In the first place, his sub-genus *Tachybaptus* is probably not a wholly monophyletic group for *Podiceps dominicus* does not appear to belong there: it is a New World form, whereas *P. ruficollis* and its allies are Old World, and its plumage is very different (see also Storer 1960). Nor does there seem good reason to combine the true dabchicks with the two hoary-headed grebes, *P. poliocephalus* and *P. rufopectus*, of the subgenus *Poliocephalus*. These two seem to be much closer to *P. occipitalis* and its allies from South America.

I have retained all these small grebes in the genus *Podiceps* for the time being, placing *P. ruficollis* and its allies in one species group, *P. dominicus* by itself in another, and transferring the two *Poliocephalus* grebes to the species group containing the typical ornamented grebes (see further under *Podiceps* below). If the latter regrouping is acceptable, the name *Poliocephalus* will thus not be available in future for the Old World dabchicks. The affinities of *P. dominicus* are uncertain. Further work may indicate that it should be placed in a monotypic genus of its own, following a course already favoured for the other peculiar American grebes of the genera *Podilymbus* and *Aechmophorus*. Should this solution be thought to be the correct one, then the true dabchicks could also be separated from *Podiceps* as the genus *Sylbeocyclus* Macgillivray, 1842 (which has priority over *Tachybaptus* Reichenbach, 1853, used by Peters 1931). However, until the status of *P. dominicus* is certain, it seems best to leave all these small grebes in the genus *Podiceps*.

Podiceps

This genus raises many problems, some of which have already been mentioned. The modern tendency (followed here) has been to place the majority of the grebes in *Podiceps* and this gives an impression of unbalance to the classification of the Podicipitidae. Yet the maintenance of a large genus *Podiceps* seems to be the best course at the present state of knowledge, for clearly this genus represents the major adaptive radiation of the grebes. I have divided it into four species groups, resisting the temptation of erecting further genera or subgenera, which would give a false impression of finality to the arrangenemt. The groups themselves seem definite enough but their inter-relations are not yet fully clear. The problem of *P. dominicus* has already been mentioned. A similar doubt exists as to the affinities of the two grey-faced grebes, *P. major* and *P. grisegena*. The latter is almost traditionally associated in various works with *P. cristatus* and its allies. However, the head-ornamentation of both *P. major* and *P. grisegena* is distinctive and apparently represents a trend similar to that in the true dabchicks (especially *P. rufolavatus* and *P. pelxelnii*) rather than that in the typical ornamented grebes. If the dabchicks and *P. dominicus* were removed from *Podiceps*, then it might be necessary also to remove *P. major* and *P. grisegena* to form a third genus *Pedetaithya* Kaup, 1829, leaving the typical ornamented grebes in sole possession of a reduced genus *Podiceps* (of which *P. cristatus* is the type species). The latter grebes are a well-knit group phylogenetically, falling into two main sub-groups, with *P. auritus* and *P. cristatus* both standing

somewhat apart. *P. occipitalis* and *P. taczanowskii* and *P. nigricollis* and *P. andinus* are obviously closely related, having many similarities in morphology and behaviour which are shared, at least to some extent, by the two hoary-headed grebes *P. poliocephalus* and *P. rufopectus*. The two latter may well belong within the same sub-group as *P. occipitalis* and its allies but, until more information is available, I think it safer to leave them as a separate sub-group next to the other. I am convinced that *P. micropterus* belongs to the same species group as *P. chilensis* and *P. rolland*, representing an earlier colonization of Lake Titicaca by *P. chilensis*, or its immediate ancestor, just as *P. rolland* represents a more recent colonization of the Falkland Islands by *P. chilensis* stock. Both *P. micropterus* and *P. rolland* have increased appreciably in size but, while the latter has retained a nuptial plumage identical with that of *P. chilensis* and remained capable of flight (at least when not at maximum weight), *P. micropterus* has become flightless and developed a nuptial plumage that is merely an elaboration of the eclipse plumage of *P. chilensis*.

A final point. *P. nigricollis* has sometimes been placed in the genus *Proctopus* Kaup, 1829, by writers on Ethiopian birds (e.g. Roberts 1919). I can see no justification for this step. The type-species of *Proctopus* is, by monotypy, *P. auritus* and there seems no good reason for supposing there to be a closer relationship between *P. nigricollis* and *P. auritus* than between either and *P. cristatus*, the type species of the genus *Podiceps*. If the genus *Proctopus* were to be upheld, then to be consistent, one would have to erect a genus for practically every other species of grebe. (N.B. The genus *Dytes* Kaup, 1829, has page priority over the genus *Proctopus* Kaup, 1829; the type species of *Dytes* is also *P. auritus*.)

Pairs of very closely related forms

Within the Podicipitidae, there are a number of very closely related forms. The following are sympatric over at least part of the range:

(1) *Podiceps ruficollis* and *P. novaehollandiae;*
(2) *P. ruficollis* and *P. rufolavatus* (though the former is rare on Madagascar and there seems no evidence that the two forms ever actually meet);
(3) *P. rufolavatus* and *P. pelzelnii* (again, there is no evidence, so far as I am aware, that the two forms ever actually meet on Madagascar);
(4) *P. occipitalis* and *P. taczanowskii.*

The following pairs are entirely allopatric:

(1) *P. nigricollis* and *P. andinus;*
(2) *P. chilensis* and *P. rolland;*
(3) *Podilymbus podiceps* and *P. gigas.*

There is no choice, of course, but to treat each member of the sympatric pair as a full species, the two forming a "species-pair". In the case of *Podiceps ruficollis* and *P. rufolavatus* and of *P. rufolavatus* and *P. pelzelnii*, the forms show noticeable morphological differences from each other. With the siblings *P. ruficollis* and *P. novaehollandiae* and *P. occipitalis* and *P. taczanowskii*, however, there is much closer morphological similarity

so that, if they were allopatric instead of sympatric, a decided problem of whether or not to combine them in single species would be posed. This fact should be taken into account, therefore, in assessing the status of the allopatric pairs. In each case, there is a widespread, polytypic species (*P. nigricollis*, *P. chilensis* and *Podilymbus podiceps*) and a geographically isolated form (*Podiceps andinus*, *P. rolland* and *Podilymbus gigas*), clearly the representative of the other but distinct to some extent in plumage and/or structure. My first inclination was to lump them into single species and such a procedure would certainly be followed by many modern taxonomists. However, the isolate of the allopatric pair is at least a developing species and should not, in my opinion, be submerged taxonomically by being treated as a mere race of the wider ranging form. The small differences within the latter are transcended by the greater difference between it and the isolate in every case.

The geographically isolated forms are "semispecies" in the sense of Mayr (1940). They have to be treated binomially. For this reason, the category is rather unsatisfactory, for it is impossible to characterize semispecies within our present system of nomenclature, so they emerge in practice as binomial forms indistinguishable from monotypic, but undoubtedly full species. Further, forms treated as semispecies are likely to differ in status; some may be full species, others not—we are just in no position to know. Nevertheless, the category of the semispecies for very distinctive forms is preferable to terming these forms subspecies or to raise them unequivocally to the status of full species.

Superspecies

A semispecies and its related, wider ranging form constitute at least a simple superspecies of the first stage of differentiation. As discussed above, there are three such incipient superspecies within the Podicipitidae. In addition, some better defined superspecies may be recognized:

(1) *Podiceps major* and *P. grisegena;*

(2) *P. poliocephalus* and *P. rufopectus;*

(3) *P. nigricollis/andinus* with both *P. occipitalis* and *P. taczanowskii* (the situation here being somewhat complicated by the fact that the two latter species are sympatric).

A REVISED CHECK-LIST OF THE GREBES

Notes:

(1) Semispecies have been bracketted with their related, wider ranging form.

(2) Superspecies are designated by the names of the terminal species.

(3) Forms marked by an asterisk are full, polytypic species; those unmarked are full, monotypic species, while semispecies are distinguished by italics.

(4) In the case of the genus *Podiceps*, I have indicated in brackets the generic or subgeneric name available to any species group or subgroup, together with the type species, in case that group be eventu-

ally given formal nomenclatural status (no name seems available for *P. dominicus*).

(5) The range given under each form is only a rough guide to the main area(s) of distribution.

Genus PODILYMBUS Lesson, 1831

*P. podiceps (Linnaeus, 1758)
North and South America.
P. gigas Griscom, 1929
Lake Atitlan, Guatemala.

Genus PODICEPS Latham, 1787

Species group A (Sylbeocyclus Macgillivray, 1842: P. ruficollis)

*P. ruficollis (Pallas, 1764)
Europe, Asia, Africa, some Australasian islands.
*P. novaehollandiae Stephens, 1826
Tasmania, Australia, some Australasian islands.
P. rufolavatus Delacour, 1933
Madagascar (confined to the Lake Alaotra area).
P. pelzelnii Hartlaub, 1861
Madagascar generally.

Species group B

*P. dominicus (Linnaeus, 1766)
Southern North America, South America.

Species group C (Pedetaithya Kaup, 1829: P. grisegena)

Superspecies P. major-grisegena
P. major (Boddaert, 1783)
Southern half of South America.
*P. grisegena (Boddaert, 1783)
North America, Europe, Asia.

Species group D (Podiceps Latham, 1787: P. cristatus)

Sub-group 1 (Rollandia Bonaparte, 1853: P. rolland)

*P. chilensis Lesson, 1828
Southern half of South America (north to eastern Peru).
P. rolland Quoy & Gaimard, 1824
Falkland Islands.
P. micropterus Gould, 1868
Lake Titicaca basin, Peru and Bolivia.

Sub-group 2 (Dytes Kaup, 1829: P. auritus)

*P. auritus (Linnaeus, 1758)
North America, Europe, Asia.

Sub-group 3 (Poliocephalus Selby, 1840: P. poliocephalus)

Superspecies P. poliocephalus-rufopectus
*P. poliocephalus Jardine & Selby, 1827
Tasmania, Australia.

P. rufopectus Gray, 1843
New Zealand.

Sub-group 4 (Calipareus Gray, 1871: P. occipitalis)

Superspecies P. occipitalis-nigricollis

*P. occipitalis Garnot, 1826
Southern South America (north to southern Colombia), Falkland Islands.

P. taczanowskii Berlepsch & Stolzmann, 1894
Lake Junin, Peru.

*P. nigricollis Brehm, 1831
North America, Europe, Asia, Africa.

P. andinus (de Schauensee, 1959)
Eastern Andes of northern Colombia.

Sub-group 5 (Podiceps Latham, 1787: P. cristatus)

*P. cristatus (Linnaeus, 1758)
Europe, Asia, Africa, Australia, New Zealand.

Genus AECHMOPHORUS Coues, 1862

A. occidentalis (Lawrence, 1858)
North America.

References:

Delacour, J. 1933. *L'oiseau* 3: 4–7.
Goodwin, D. 1959. *Bull. Brit. Mus.* (*Nat. Hist.*) 6 (1).
Gould, J. 1868. *Proc. Zool. Soc. London:* 220–221.
Hellmayr, C. E. and Conover, B. 1948. *Pub. Field Mus. Nat. Hist.* (*Zool. series*) 13, 1 (2).
International Commission on Zoological Nomenclature 1956. *Opinions and declarations* 13 (1): 1–46.
Peters, J. L. 1931. *Check-list of birds of the world*, 1. Cambridge (Mass.).
Mayr, E. 1940. *Amer. Nat.* 74: 249–278.
Mayr, E. 1943. *Emu* 43: 3–17.
Parkes, K. C. 1952. *Condor* 54: 314–315.
Roberts, A. 1919. *Ann. Transvaal Mus.* 6: 118.
de Schauensee, R. M. 1959. *Proc. Acad. Nat. Sci. Philadelphia* 111: 55.
Sclater, P. L. and Salvin, O. 1869. *Exotic ornithology, containing figures and descriptions of new or rare species of American birds.* London.
Simmons, K. E. L. 1954. *Bird Study* 1: 53–56.
Simmons, K. E. L. 1955. Studies on Great Crested Grebes. *Avicult. Mag.*, London.
Simmons, K. E. L. 1959. In Bannerman's *Birds of the British Isles* 8: 215–223.
Storer, R. W. 1960. *Proc. XII Internat. Orn. Cong. Helsinki* 1958: 695–707.
Wetmore, A. and Parkes, K. C. 1954. *J. Washington Acad. Sci.* 44: 126–127.